Wilson Bull., 108(4), 1996, pp. 685–696

GRIT-USE PATTERNS IN NORTH AMERICAN BIRDS: THE INFLUENCE OF DIET, BODY SIZE, AND GENDER

JAMES P. GIONFRIDDO[1,2] AND LOUIS B. BEST[1]

ABSTRACT.—We investigated avian grit use by examining the gizzard contents of 1440 birds collected from 12 states. Grit was present in gizzards of 62 of 90 species and varied greatly in number and mean particle size. Gizzards of granivorous birds contained more grit particles than those of insectivores, omnivores, and frugivores. Grit particle characteristics (mean size, shape, and surface texture) did not differ among birds consuming different diets. Mean grit size increased linearly with the common logarithm of the bird body mass. Within avian species, grit-use patterns did not differ by gender. Grit use is widespread among birds, and diet strongly influences the amount of grit used by birds. *Received 18 Oct. 1995, accepted 10 March 1996.*

Best and Gionfriddo (1991) characterized grit use by 22 species of North American birds. The impetus for that work was the relevance of grit use to avian mortality caused by ingestion of granular pesticides used to control corn rootworms and other agricultural pests (Best and Fischer 1992). Birds included in that study were limited to species that commonly use midwestern cornfields during the breeding season, when pesticides usually are applied. The present research examined grit use by a larger number of avian species, over a wider geographical area, and included many birds collected during the nonbreeding season. Our objectives were to survey grit use by a broad range of avian species and to examine the influence of diet, body size, and gender on the amounts and characteristics of grit used by birds.

METHODS

We obtained birds opportunistically from a variety of sources including road kills, collisions with windows and other objects, hunter harvests, and research projects. Birds were collected year-round and from 12 (mostly midwestern) states. We removed the gizzards from all collected birds and preserved them in ethanol. Later, each gizzard was sliced in half and its contents were flushed into a petri dish and examined under a stereomicroscope. We separated all grit particles from the other gizzard contents and excluded particles <0.1 mm in size because (1) the size distributions of grit in the gizzards of most species showed that as grit size decreased toward 0.1 mm, the number of particles per size class declined abruptly (Best and Gionfriddo 1991), and (2) we felt that particles <0.1 mm probably represented soil ingested incidentally during foraging. We then systematically counted the grit and characterized particles on the basis of size, shape, and surface texture. The longest and shortest dimensions of each particle in the 1440 gizzards we examined were measured to the nearest

[1] Dept. of Animal Ecology, Iowa State Univ., Ames, Iowa 50011.
[2] Present address: Dept. of Forestry and Natural Resources, Purdue Univ., West Lafayette, Indiana 47907.

0.1 mm with a digital caliper or an ocular micrometer in the microscope. We used the average of these two values as a measure of particle size and their ratio as a shape index value. Shape index values were ≥1.0, with 1.0 representing a somewhat spherical shape and larger values representing more oblong shapes. We characterized the surface texture of each grit particle in 499 of the gizzards by using a classification system developed by petrologists to describe mineral grains (fig. 1 in Best and Gionfriddo 1991). The five surface-texture categories were angular, sub-angular, sub-rounded, rounded, and well-rounded. An overall mean surface-texture value was calculated for each bird by assigning particles in the angular category a value of 1, those in the sub-angular category a value of 2, etc.

For comparisons of grit use based on diet, we classified each bird as an insectivore, granivore, omnivore, frugivore, or carnivore, taking into account the month in which the bird was collected and following the classification of DeGraaf et al. (1985). We classified Ring-necked Pheasants (scientific names of avian species are in Table 1) collected during the non-breeding season, however, as granivores (rather than herbivores, as suggested by DeGraaf et al. [1985]) because most of their non-breeding season diet consists of seeds (e.g., Dalke 1937, Ferrel et al. 1949, Korschgen 1964). Carnivores and frugivores were excluded from some analyses because of small sample sizes.

Except for the diet-based comparisons (in which data from species with similar diets were combined), our analyses of grit use were limited to those species for which the contents of at least five gizzards were examined. This limitation was imposed because of the great intraspecific variation in the number of grit particles per gizzard, a variable for which there is only one value per gizzard. For other variables, such as grit size, shape, or surface texture, each gizzard yielded as many values per variable as there were grit particles in the gizzard.

Bird body masses were obtained from Dunning (1993). For dimorphic species used in intraspecific comparisons by gender (i.e., species with ≥5 birds of each gender included in the sample), we assigned the gender-specific masses given by Dunning (1993). For the other dimorphic species, we assigned to each bird the mean of Dunning's values for males and females.

Analysis of variance (ANOVA) was used to identify differences in grit use among birds consuming different types of foods. When ANOVA detected differences among dietary groups, we used Student-Newman-Keuls (SNK) multiple comparison tests to identify specifically which groups differed. Using data only from those species for which we examined the contents of ≥5 gizzards, we calculated Pearson product-moment correlations to examine if the mean number of grit particles per gizzard was related to grit occurrence (the percentage of gizzards containing grit) or mean grit size. We used regression analysis to examine the relationship between mean grit size and bird body size. Two-tailed t-tests were used to examine if mean grit counts, sizes, shape index values, or surface-texture values differed by gender. Unless otherwise indicated, a significance level of $P \leq 0.05$ was used for statistical tests.

RESULTS

Gizzard contents of birds representing 90 species and 10 orders were examined. Grit was present in gizzards of 62 species (9 orders). Frequencies of occurrence of grit in gizzards and grit counts per gizzard varied greatly among species. Species with low frequencies of occurrence of grit (and low grit counts) generally were insectivores, whereas those with high frequencies of occurrence (and high grit counts) usually were granivores. Among the 35 avian species for which ≥five gizzards were examined, frequencies of grit occurrence in gizzards ranged from 0 to 100%, and mean grit counts per gizzard ranged from 0 to 281 (Table 1). Gizzards of Ring-necked Pheasants, American Tree Sparrows, and House Sparrows had the highest frequencies of occurrence of grit and also generally had the highest grit counts. Low frequencies of occurrence and grit counts were recorded for Eastern Kingbirds, Cedar Waxwings, Barn Swallows, Dickcissels, Common Yellowthroats, Yellow-rumped Warblers, and Northern Orioles. Grit occurrence and mean grit counts were correlated ($r = 0.502$). Intraspecific variation in grit counts was substantial: standard deviations typically exceeded mean values (Table 1).

Mean grit counts per gizzard differed among birds consuming different foods ($F_{3,1432} = 59.01$, $P < 0.001$). Gizzards of granivores contained more grit particles than those of insectivores, omnivores, and frugivores (SNK test, $P \leq 0.05$) (carnivores were excluded because of small sample size). The adjusted mean grit size (see below), mean shape index value, and mean surface-texture value did not differ among granivores, insectivores, and omnivores (size: $F_{2,969} = 2.41$, $P = 0.090$; shape: $F_{2,969} = 0.691$, $P = 0.501$; surface texture: $F_{2,490} = 2.455$, $P = 0.087$). Carnivores and frugivores were excluded because of small sample sizes.

Regression analysis indicated that mean grit size was related to bird body size, increasing linearly with the $\log_{(10)}$ of the body mass (Fig. 1). To permit examination of the relationships between mean grit size and other variables (with the effects of bird body size partitioned out), we adjusted the mean grit size for each species by adding the species' residual value to the overall mean grit size of the sample (Steel and Torrie 1980: 251). For most (22) of the 33 grit-using species for which we examined ≥five gizzards, there was no detectable relationship between the adjusted mean grit size and the number of grit particles per gizzard. In 11 species, however, a significant ($P \leq 0.01$) negative correlation was found between these variables.

Among the 17 species for which we examined ≥5 gizzards for each gender (Table 1), mean grit counts differed ($P \leq 0.05$) intraspecifically by gender only in Ring-necked Pheasants ($t = 3.40$, 31 df, $P = 0.002$) and Red-headed Woodpeckers ($t = 2.45$, 16 df, $P = 0.026$). In both species, gizzards of females contained more grit than those of males. Gender comparisons of adjusted mean grit sizes, mean shape index values, and mean surface-texture values detected few differences. Because surface-texture values were calculated only for 499 birds, sample sizes permitted gender comparisons within only five species: Northern Bobwhite, Brown-headed Cowbird, Red-winged Blackbird, Vesper Sparrow, and House Sparrow. In Brown-headed Cowbirds, females used larger ($t = 2.97$, 87 df, $P = 0.004$), less oblong ($t = 2.72$, 87 df, $P = 0.008$), and

TABLE 1
GRIT USE BY WILD BIRDS[a]

Species	Dietary class[b]	Gizzards sampled	Occurrence (%)[c]	Count[d] $\bar{x} \pm SD$	Count[d] Median	Mean size (mm)	Shape index[e]	Surface texture[e,f]
Ring-necked Pheasant (*Phasianus colchicus*)	G	37[g]	100	151 ± 190	88	2.3	2.0	3.3
Ring-necked Pheasant (*P. colchicus*)	O	4[g]	100	381 ± 258	430	1.7	1.8	3.1
Northern Bobwhite (*Colinus virginianus*)	O	75[g]	90	49 ± 106	12	1.8	1.8	3.1
Killdeer (*Charadrius vociferus*)	I	28[g]	93	8 ± 9	5	1.9	2.1	2.6
Rock Dove (*Columba livia*)	O	15	100	69 ± 43	60	2.3	2.0	3.3
Mourning Dove (*Zenaida macroura*)	G	40	68	10 ± 16	3	2.1	1.7	3.0
Yellow-billed Cuckoo (*Coccyzus americanus*)	I	9	44	3 ± 6	0	1.6	1.8	3.0
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	I	27[g]	57	31 ± 59	2	0.9	1.8	3.0
Eastern Kingbird (*Tyrannus tyrannus*)	I	29[g]	24	1 ± 4	0	1.3	1.9	2.7
Barn Swallow (*Hirundo rustica*)	I	23	22	1 ± 4	0	1.2	3.1	—
Horned Lark (*Eremophila alpestris*)	O	69[g]	99	11 ± 13	8	1.2	1.7	3.0
Blue Jay (*Cyanocitta cristata*)	O	20[g]	85	35 ± 42	15	1.6	2.1	2.8
American Crow (*Corvus brachyrhynchos*)	O	64[g]	53	49 ± 156	2	2.9	1.7	3.1
Cedar Waxwing (*Bombycilla cedorum*)	F	20	20	9 ± 40	0	0.3	1.7	2.9
Hermit Thrush (*Catharus guttatus*)	I	3	100	129 ± 163	54	0.3	1.7	3.0
Hermit Thrush (*C. guttatus*)	O	6	83	14 ± 17	6	0.3	1.8	2.7
American Robin (*Turdus migratorius*)	O	43[g]	44	12 ± 26	0	0.8	2.3	2.7
European Starling (*Sturnus vulgaris*)	O	56[g]	36	21 ± 85	0	1.0	1.8	2.7
House Wren (*Troglodytes aedon*)	I	7	57	3 ± 5	1	0.3	1.7	3.0
House Sparrow (*Passer domesticus*)	G	146[g]	98	281 ± 476	97	0.7	1.9	2.9
Yellow-rumped Warbler (*Dendroica coronata*)	I	5	0	0	0	—	—	—
Common·Yellowthroat (*Geothlypis trichas*)	I	14	21	1 ± 2	0	0.3	1.8	2.8
Fox Sparrow (*Passerella iliaca*)	G	5	100	102 ± 88	93	0.5	2.0	3.1
Song Sparrow (*Melospiza melodia*)	O	14	93	14 ± 15	8	0.8	1.8	2.9
Savannah Sparrow (*Passerculus sandwichensis*)	G	21[g]	100	41 ± 102	20	1.0	2.0	3.0

TABLE 1
CONTINUED

Species	Dietary class[b]	Gizzards sampled	Occurrence (%)[c]	Count[d]		Mean size (mm)	Shape index[e]	Surface texture[e,f]
				$\bar{x} \pm$ SD	Median			
Savannah Sparrow (*P. sandwichensis*)	O	5[g]	60	50 ± 80	22	0.7	1.9	3.4
American Tree Sparrow (*Spizella arborea*)	G	8	100	267 ± 212	203	0.4	1.9	3.1
Chipping Sparrow (*S. passerina*)	O	20	95	12 ± 16	7	0.9	2.1	2.9
Vesper Sparrow (*Pooecetes gramineus*)	O	125[g]	86	12 ± 14	8	0.9	1.8	3.1
Lark Sparrow (*Chondestes grammacus*)	O	5	100	42 ± 50	22	0.6	1.8	3.2
Dickcissel (*Spiza americana*)	O	28	25	4 ± 18	0	0.8	2.0	3.2
Northern Cardinal (*Cardinalis cardinalis*)	O	22[g]	73	40 ± 82	6	1.0	2.6	2.9
Indigo Bunting (*Passerina cyanea*)	O	21	81	35 ± 91	4	0.9	1.8	2.8
Northern Oriole (*Icterus galbula*)	O	5	0	0	0	—	—	—
Red-winged Blackbird (*Agelaius phoeniceus*)	O	82[g]	73	17 ± 61	4	1.1	1.8	3.0
Western Meadowlark (*Sturnella neglecta*)	I	9	44	2 ± 3	0	1.4	1.8	3.0
Common Grackle (*Quiscalus quiscula*)	O	47[g]	57	10 ± 21	1	0.9	2.2	2.9
Brown-headed Cowbird (*Molothrus ater*)	O	175[g]	52	10 ± 30	1	1.0	2.0	2.9

[a] Includes only those species for which ≥5 gizzards were sampled.
[b] Based on month of capture, using classification of DeGraaf et al. (1985). I = insectivore, G = granivore, O = omnivore, and F = frugivore.
[c] The percentage of gizzards in which grit particles were present.
[d] The number of grit particles per gizzard.
[e] See text for a description of how these values were derived.
[f] This variable was called "roundness" in Best and Gionfriddo (1991).
[g] These 17 species were used for intraspecific, gender comparisons of grit use.

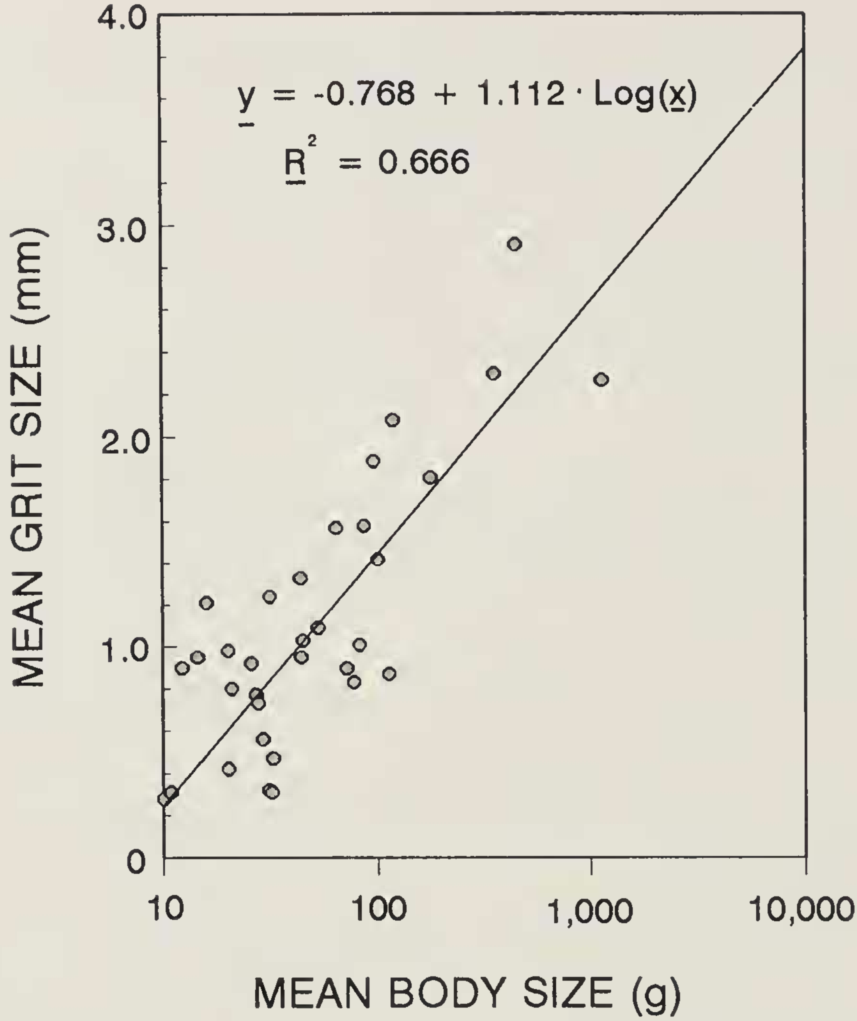

FIG. 1. Relationship between mean grit size and mean bird body mass. Body masses were obtained from Dunning (1993). Each point represents a species for which the contents of at least five gizzards were examined.

more angular (t = 2.38, 43 df, P = 0.022) grit than males. Female Ring-necked Pheasants and Horned Larks used smaller grit than males (pheasants: t = 2.48, 31 df, P = 0.019; larks: t = 2.10, 28 df, P = 0.045).

DISCUSSION

The most commonly proposed function of avian grit use is the facilitation of mechanical grinding and pulverization of food in the gizzard (Meinertzhagen 1964, Ziswiler and Farner 1972). Grit also may provide supplementary minerals, especially calcium (e.g., Korschgen 1964, Norris et al. 1975, Turner 1982). Avian grit use often varies with such factors as the bird's diet (e.g., Mott et al. 1972, Norris et al. 1975, Alonso 1985, Bishton 1986), age (Bartonek 1969, Verbeek 1970, Alonso 1985, Mayoh and Zach 1986), body size (Best and Gionfriddo 1991), and gender and reproductive status (e.g., Harper 1964, Kopischke and Nelson 1966, May and Braun 1973, Pinowska and Kraśnicki 1985), as well as with the availability of suitable grit particles (Bump et al. 1947, Tindall 1973, Norris et al. 1975).

Diet is a major factor influencing avian grit use. Grit generally is found in the gizzards of most species that eat plant material (Farner 1960, Meinertzhagen 1964) and many that eat insects (e.g., Barlow et al. 1963, Jenkinson and Mengel 1970, Barrentine 1980, Mayoh and Zach 1986). Relatively large amounts of grit often are associated with diets consisting of hard, coarse materials, especially seeds and other plant parts (Meinertzhagen 1954, Farner 1960). Insectivores often use less grit than herbivorous or granivorous birds (Mott et al. 1972, Bishton 1986, Hogstad 1988), and frugivores typically use little grit (Meinertzhagen 1954, 1964). The amounts of grit needed by insectivores and granivores may depend on the hardness of the items consumed. The digestion of soft-bodied insect larvae, for example, may require relatively little grit, whereas the breakdown of hard-bodied insects (e.g., adult coleopterans) may require large amounts (Pinowska 1975, Gionfriddo and Best 1995). Grit-sized hard insect fragments (e.g., Bird and Smith 1964, Jenkinson and Mengel 1970, Mott et al. 1972) or hard seeds (e.g., Beer and Tidyman 1942, Sharp and McClure 1945, Lewin and Lewin 1984) are sometimes retained in the gizzard where they serve as grit substitutes by aiding in the mechanical grinding of softer foods. When such grit substitutes are present in gizzards, less grit is required. Hard insect parts or hard seeds were present in some of the gizzards we examined, and therefore, in some cases, our grit counts may underestimate the birds' need for grit.

Our finding no differences in adjusted mean grit size, mean grit shape, and mean grit surface texture among birds consuming different diets suggests that different foods may not require grit with different physical characteristics for adequate digestion. The characteristics of grit particles in birds' gizzards are influenced by avian preferences and aversions (Best and Gionfriddo 1994), the availability of grit particles with different characteristics (Bump et al. 1947, Tindall 1973, Norris et al. 1975), and rates of breakdown and passage of grit from the gizzards (Lienhart 1953, Korschgen et al. 1965, Vance 1971, Norris et al. 1975, Gionfriddo and Best 1995).

The large amounts of grit we observed in gizzards of Ring-necked Pheasants, American Tree Sparrows, and House Sparrows were not surprising because these species feed mainly on seeds on the ground. The relatively low grit counts and frequencies of occurrence of grit in gizzards of Eastern Kingbirds, Barn Swallows, and Cedar Waxwings were expected because these species feed on insects or fruits, aerially or in trees.

The other species that tended to use little or no grit (Common Yellowthroat, Yellow-rumped Warbler, Northern Oriole) also glean insects in trees or shrubs. The finding that Dickcissels used little grit on their North American breeding grounds is consistent with Zimmerman's (1963) report that wintering Dickcissels in central America used relatively large amounts of grit, but that breeding birds in Illinois used little. Zimmerman (1963) attributed the difference to the Dickcissels' heavier use of insects in North America and seeds in central America. Field studies of other avian species that shift diets seasonally also have documented corresponding shifts in grit use (Bishton 1986, Hogstad 1988, Gionfriddo and Best 1995). Investigation of seasonal patterns of grit use by additional species that shift diets seasonally would further clarify the relationship between grit use and diet.

The observed log-linear relationship between mean grit size and bird body mass is similar to that reported for 19 avian species collected mainly in the Midwest during the breeding season (Best and Gionfriddo 1991). Augmenting the earlier sample by including birds representing many additional avian taxa, geographical locations, and seasons did not substantially alter the linear model describing this relationship. The lack of a strong relationship between mean grit size and mean grit count for most (22 of 33) species we tested differs from the results of other field (Myrberget et al. 1975, Norris et al. 1975, Alonso 1985, Best and Gionfriddo 1991) and laboratory (McCann 1939, Smith 1960, Gionfriddo and Best 1995) studies which found that the larger the grit particles, the fewer were present in gizzards. The current finding is consistent, however, with the results of a diet experiment with captive House Sparrows (Gionfriddo and Best 1995).

Grit use by males and females often is reported to be similar (e.g., Alonso 1985, Norman and Brown 1985, Garcher and Carroll 1991, Gionfriddo and Best 1995). When differences exist, they sometimes are due to differences in body size (Rajala 1958, Pulliainen 1979, Norman and Mumford 1985) or to females' increased calcium requirements during egg laying (Sadler 1961, Harper 1964, Taylor 1970). Females may greatly increase their consumption of grit during the egg-laying period (Pinowska and Kraśnicki 1985), and/or they may selectively consume calcium-rich grit particles (Harper 1964, Korschgen 1964, Kopischke and Nelson 1966). Such reproduction-related changes in grit use (and gender differences that result from them) may be short-lived (Pinowska and Kraśnicki 1985), however, and therefore probably would not have been detectable in our study.

In addition to demonstrating the importance of diet and body size as factors affecting avian grit use, our study shows that grit use is widespread among birds, both taxonomically and geographically. Moreover, although the collection of birds for this research was not limited geographically or temporally to areas or seasons of application of granular pesticides, our results nonetheless have important implications for the design and use of such products. Granular pesticides are applied to millions of hectares of agricultural crops in North America each year (U.S. Dept. Agric. 1992). Many of these pesticides are acutely toxic to birds (Balcomb et al. 1984, Hill and Camardese 1984), and one potential route of avian exposure is consumption of granules as a source of grit. Our results indicate that, if this is an important route of avian exposure to granular pesticides, then in pesticide-treated areas granivorous birds (including such important game species as the Ring-necked Pheasant and Northern Bobwhite) may have a relatively high risk of exposure because they use more grit than birds that eat other foods. Our results confirm that altering granule size to reduce avian risk is not likely to be effective. The wide range of grit sizes used by birds, and the extensive interspecific overlap in grit sizes result in there being no "safe" granule size that would be infrequently used by birds, given the upper and lower limits to pesticide granule size imposed by other factors, such as human safety and ease of application.

ACKNOWLEDGMENTS

We thank K. L. Andersen, K. K. Aulwes, B. M. Ballard, C. Best, J. D. Best, N. Best, J. R. Gionfriddo, J. M. Grady, D. S. Huntrods, L. D. Igl, A. L. Linville, F. D. Zenitsky, and G. D. Zenitsky for assisting with laboratory work and data tabulation. We are grateful to those who provided or collected birds for our study, especially J. J. Dinsmore, B. J. Giesler, L. D. Igl, D. W. DeGeus, D. S. Huntrods, and G. M. Booth. We appreciate the cooperation of state and federal agencies in granting permission for collection of birds. We thank C. E. Braun, J. J. Dinsmore, E. E. Klaas, J. L. Sell, K. C. Shaw, D. W. White, and C. R. Blem for reviewing earlier drafts of the manuscript and offering helpful suggestions. Funding was provided by Miles, Inc., Rhône-Poulenc, American Cyanamid, and Dow Elanco. This is Journal Paper No. J-16181 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Project 2168.

LITERATURE CITED

ALONSO, J. C. 1985. Grit in the gizzard of Spanish Sparrows (*Passer hispaniolensis*). Vogelwarte 33:135–143.

BALCOMB, R., R. STEVENS, AND C. BOWEN II. 1984. Toxicity of 16 granular insecticides to wild-caught songbirds. Bull. Environ. Contam. Toxicol. 33:302–307.

BARLOW, J. C., E. E. KLAAS, AND J. L. LENZ. 1963. Sunning of Bank and Cliff swallows. Condor 65:438–440.

BARRENTINE, C. D. 1980. The ingestion of grit by nestling Barn Swallows. J. Field Ornithol. 51:368–371.

BARTONEK, J. C. 1969. Build-up of grit in three pochard species in Manitoba. Wilson Bull. 81:96–97.

Beer, J. and W. Tidyman. 1942. The substitution of hard seeds for grit. J. Wildl. Manage. 6:70–82.

Best, L. B. and D. L. Fischer. 1992. Granular insecticides and birds: factors to be considered in understanding exposure and reducing risk. Environ. Toxicol. and Chem. 11: 1495–1508.

——— and J. P. Gionfriddo. 1991. Characterization of grit use by cornfield birds. Wilson Bull. 103:68–82.

——— and ———. 1994. Effects of surface texture and shape on grit selection by House Sparrows and Northern Bobwhite. Wilson Bull. 106:689–695.

Bird, R. D. and L. B. Smith. 1964. The food habits of the Red-winged Blackbird, *Agelaius phoeniceus,* in Manitoba. Can. Field-Nat. 78:179–186.

Bishton, G. 1986. The diet and foraging behaviour of the Dunnock *Prunella modularis* in a hedgerow habitat. Ibis 128:526–539.

Bump, G., R. W. Darrow, F. C. Edminster, and W. F. Crissey. 1947. The Ruffed Grouse: life history, propagation, management. New York State Conserv. Dept., Albany, New York.

Dalke, P. L. 1937. Food habits of adult pheasants in Michigan based on crop analysis method. Ecology 18:199–213.

DeGraaf, R. M., N. G. Tilghman, and S. H. Anderson. 1985. Foraging guilds of North American birds. Environ. Manage. 9:493–536.

Dunning, J. B., Jr., ed. 1993. CRC handbook of avian body masses. CRC Press, Boca Raton, Florida.

Farner, D. S. 1960. Digestion and the digestive system. Pp. 411–467 *in* Biology and comparative physiology of birds. Vol. 1 (A. J. Marshall, ed.). Academic Press, New York, New York.

Ferrel, C. M., H. Twining, and N. B. Herkenham. 1949. Food habits of the Ring-necked Pheasant (*Phasianus colchicus*) in the Sacramento Valley, California. Calif. Fish and Game 35:51–69.

Garcher, M. L. and J. P. Carroll. 1991. Comparative diet study of male and female Wilson's Phalaropes in North Dakota. J. Pennsylvania Acad. Sci. (Suppl.) 64:190.

Gionfriddo, J. P. and L. B. Best. 1995. Grit use by House Sparrows: effects of diet and grit size. Condor 97:57–67.

Harper, J. A. 1964. Calcium in grit consumed by hen pheasants in east-central Illinois. J. Wildl. Manage. 28:264–270.

Hill, E. F. and M. B. Camardese. 1984. Toxicity of anticholinesterase insecticides to birds: technical grade versus granular formulations. Ecotoxicol. Environ. Safety 8:551–563.

Hogstad, O. 1988. Foraging pattern and prey selection of breeding Bramblings *Fringilla montifringilla.* Fauna Norv. Ser. C, Cinclus 11:27–39.

Jenkinson, M. A. and R. M. Mengel. 1970. Ingestion of stones by goatsuckers (Caprimulgidae). Condor 72:236–237.

Kopischke, E. D. and M. M. Nelson. 1966. Grit availability and pheasant densities in Minnesota and North Dakota. J. Wildl. Manage. 30:269–275.

Korschgen, L. J. 1964. Foods and nutrition of Missouri and midwestern pheasants. Trans. North Am. Wildl. and Nat. Resour. Conf. 29:159–180.

———, G. D. Chambers, and K. C. Sadler. 1965. Digestion rate of limestone force-fed to pheasants. J. Wildl. Manage. 29:820–823.

Lewin, V. and G. Lewin. 1984. The Kalij Pheasant, a newly established game bird on the island of Hawaii. Wilson Bull. 96:634–646.

Lienhart, R. 1953. Recherches sur le role des cailloux contenus dans le gésier des oiseaux granivores. Bull. Soc. Sci. Nancy 12:5–9.

MAY, T. A. AND C. E. BRAUN. 1973. Gizzard stones in adult White-tailed Ptarmigan (*Lagopus leucurus*) in Colorado. Arctic and Alpine Res. 5:49–57.

MAYOH, K. R. AND R. ZACH. 1986. Grit ingestion by nestling Tree Swallows and House Wrens. Can. J. Zool. 64:2090–2093.

MCCANN, L. J. 1939. Studies of the grit requirements of certain upland game birds. J. Wildl. Manage. 3:31–41.

MEINERTZHAGEN, R. 1954. Grit. Bull. Br. Ornithol. Club 74:97–102.

———. 1964. Grit. Pp. 341–342 *in* A new dictionary of birds (A. L. Thomson, ed.). McGraw-Hill, New York, New York.

MOTT, D. F., R. R. WEST, J. W. DE GRAZIO, AND J. L. GUARDINO. 1972. Foods of the Red-winged Blackbird in Brown County, South Dakota. J. Wildl. Manage. 36:983–987.

MYRBERGET, S., C. NORRIS, AND E. NORRIS. 1975. Grit in Norwegian *Lagopus* spp. Norwegian J. Zool. 23:205–212.

NORMAN, F. I. AND R. S. BROWN. 1985. Gizzard grit in some Australian waterfowl. Wildfowl 36:77–80.

——— AND L. MUMFORD. 1985. Studies on the Purple Swamphen, *Porphyrio porphyrio*, in Victoria. Australian Wildl. Res. 12:263–278.

NORRIS, E., C. NORRIS, AND J. B. STEEN. 1975. Regulation and grinding ability of grit in the gizzard of Norwegian Willow Ptarmigan (*Lagopus lagopus*). Poult. Sci. 54:1839–1843.

PINOWSKA, B. 1975. Food of female House Sparrows (*Passer domesticus* L.) in relation to stages of the breeding cycle. Polish Ecol. Stud. 1:211–225.

——— AND K. KRAŚNICKI. 1985. Quantity of gastroliths and magnesium and calcium contents in the body of female House Sparrows during their egg-laying period. Zesz. Nauk. Filii UW, 48, Biol. 10:125–130.

PULLIAINEN, E. 1979. Grit intake of the Capercaillie, *Tetrao urogallus*, in the northern Finnish taiga in autumn. Aquilo Ser. Zool. 19:45–47.

RAJALA, P. 1958. The choice of grinding stones by Capercaillie, Black Grouse, and ptarmigan in the light of enclosure experiments. Suomen Riista 12:89–93.

SADLER, K. C. 1961. Grit selectivity by the female pheasant during egg production. J. Wildl. Manage. 25:339–341.

SHARP, W. M. AND H. E. MCCLURE. 1945. The pheasant in the sandhill region of Nebraska. Pp. 203–233 *in* The Ring-necked Pheasant and its management in North America (W. L. McAtee, ed.). Am. Wildl. Inst., New York, New York.

SMITH, R. E. 1960. The influence of size and surface condition of grit upon the digestibility of feed by the domestic fowl. Can. J. Anim. Sci. 40:51–56.

STEEL, R. G. D. AND J. H. TORRIE. 1980. Principles and procedures of statistics: a biometrical approach, 2nd ed. McGraw-Hill, New York, New York.

TAYLOR, T. G. 1970. The provision of calcium and carbonate for laying hens. Pp. 108–117 *in* Proc. Univ. Nottingham Fourth Nutrition Conf. for Feed Manufacturers (H. Swan and D. Lewis, eds.). J. and A. Churchill, London, U.K.

TINDALL, A. R. 1973. Gastroliths in Norwegian grouse (*Lagopus lagopus*). Acta Physiol. Scand., Suppl. 396:66.

TURNER, A. K. 1982. Timing of laying by swallows (*Hirundo rustica*) and Sand Martins (*Riparia riparia*). J. Anim. Ecol. 51:29–46.

U.S. DEPARTMENT OF AGRICULTURE. 1992. Agricultural chemical usage: 1991 field crops survey. U.S. Dep. Agric., Econ. Res. Serv., Washington, D.C.

VANCE, D. R. 1971. Physical and chemical alterations of grit consumed by pheasants. J. Wildl. Manage. 35:136–140.

VERBEEK, N. A. M. 1970. Breeding ecology of the Water Pipit. Auk 87:425–451.

Zimmerman, J. L. 1963. The bioenergetics of the Dickcissel, *Spiza americana.* Ph.D. diss., Univ. Illinois, Urbana, Illinois.

Ziswiler, V. and D. S. Farner. 1972. Digestion and the digestive system. Pp. 343–430 *in* Avian biology. Vol. 2 (D. S. Farner, J. R. King, and K. C. Parkes, eds.). Academic Press, New York, New York.